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Morphology, ethology, new records, and ecological niche modeling for *Hydromorphus* and *Tretanorhinus* (Squamata, Colubridae) in Panama

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Abstract

The genera *Hydromorphus* and *Tretanorhinus* (Colubridae) comprise uncommon, poorly studied aquatic snakes, largely because of their nocturnal and aquatic habits. In Panama, four species have been recorded: *Hydromorphus concolor*, *H. dunni*, *Tretanorhinus mocquardi*, and *T. nigroluteus*. Although more than a century has passed since the first Panamanian record, knowledge of their distribution, morphology, ecology, and behavior remains limited. Through an exhaustive literature review and fieldwork, we updated their distribution and provided seven new records for *H. dunni*, 16 for *H. concolor*, six for *T. mocquardi*, and five for *T. nigroluteus*. For *H. dunni*, the only previously known record was the holotype from the original description. We documented substantial range extensions, especially for *H. dunni*, with new records extending its known distribution by 228 km northeast to Donoso (Colón Province) and 273 km southeast to Altos de Campana National Park, representing the most distant records for the species to date. We report new localities in Darién Province for *T. mocquardi* and in Bocas del Toro Province for *T. nigroluteus*, collectively refining the known distribution of these aquatic snakes in Panama. We identified previously unreported variation in the arrangement and number of cephalic scales, particularly in *H. dunni*, strengthening the morphological basis for taxonomic diagnosis. We also provide an updated morphological dichotomous key. In addition, we contribute to knowledge of the trophic ecology of *T. nigroluteus* by

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documenting a direct case of necrophagy during captive feeding trials. Overall, this study provides new information on these taxa in Panama, improves their ecological characterization, and may support future conservation efforts.

Resumen

Los géneros *Hydromorphus* y Tretanorhinus (Colubridae) comprenden serpientes acuáticas poco comunes y escasamente estudiadas, en gran parte debido a sus hábitos nocturnos y acuáticos. En Panamá se han registrado cuatro especies: *Hydromorphus concolor*, *H. dunni*, *Tretanorhinus mocquardi* y *T. nigroluteus*. Aunque ha pasado más de un siglo desde el primer registro panameño, el conocimiento sobre su distribución, morfología, ecología y comportamiento sigue siendo limitado. Mediante una revisión exhaustiva de la literatura y trabajo de campo, actualizamos su distribución y aportamos siete nuevos registros para *H. dunni*, dieciséis para *H. concolor*, seis para *T. mocquardi* y cinco para *T. nigroluteus*. En el caso de *H. dunni*, el único registro previamente conocido correspondía al holotipo de su descripción original. Documentamos ampliaciones sustanciales del rango de distribución, especialmente para *H. dunni*, con nuevos registros que extienden su distribución conocida 228 km al noreste hasta Donoso (provincia de Colón) y 273 km al sureste hasta el Parque Nacional Altos de Campana, representando los registros más distantes para la especie hasta la fecha. Reportamos nuevas localidades en la provincia de Darién para *T. mocquardi* y en la provincia de Bocas del Toro para *T. nigroluteus*, refinando en conjunto la distribución conocida de estas serpientes acuáticas en Panamá. Identificamos variación previamente no reportada en la disposición y número de escamas cefálicas, particularmente en *H. dunni*, fortaleciendo la base morfológica para el diagnóstico taxonómico. También proporcionamos una clave dicotómica morfológica actualizada. Además, contribuimos al conocimiento de la ecología trófica de *T. nigroluteus* al documentar un caso directo de necrofagia durante ensayos de alimentación en cautiverio. En conjunto, este estudio aporta nueva información sobre estos taxones en Panamá, mejora su caracterización ecológica y puede apoyar futuros esfuerzos de conservación.

Key Words

Colubridae, geographic distribution, morphological variation, Neotropical herpetofauna, snake ecology

Palabras clave

Colubridae, distribución geográfica, ecología de serpientes, herpetofauna neotropical, variación morfológica

Introduction

Despite decades of research on the distribution, ecology, and behavior of the ophidian fauna of Panama (Pérez-Santos 1999; Savage 2002; Köhler 2008; Jaramillo et al. 2010; Lotzkat 2014; Ray 2017; Batista and Miranda 2020), some groups remain poorly understood in terms of their natural history. Among these are the aquatic snakes of the genera *Hydromorphus* Peters, 1859 and *Tretanorhinus* Duméril, Bibron & Duméril, 1854 (Colubridae), which are uncommon and difficult to sample (Ray and Ruback 2015; García-Cobos and Vásquez-Restrepo 2022). Their aquatic and predominantly nocturnal habits have contributed to this group of snakes being one of the least studied in the Neotropical region (Lynch 2012; Melgar-Martínez et al. 2022).

Snakes of the genus *Hydromorphus* are medium-sized, reaching total lengths of 690 mm in males and 797 mm in females (Savage and Donnelly 1988; Savage 2002; Solórzano 2022). They have a rounded head, slightly differentiated from the neck, a relatively short tail, small eyes with round pupils, and nostrils oriented toward the dorsal part of the snout (Villa 1990; Solórzano 2022). *Hydromorphus* includes two species: *H. concolor* Peters, 1859, distributed from Guatemala to Colombia, and *H. dunni* Slevin, 1942, endemic to western Panama and known only from the holotype. Both are semiaquatic, inhabiting streams, rivers, creeks, and freshwater ponds (Savage and Donnelly 1988; Köhler 2008; Jaramillo et al. 2010; Lotzkat 2014; Ray 2017; Solórzano 2022).

The genus *Tretanorhinus* comprises four species distributed from Mexico to Ecuador and some Caribbean islands such as Cuba and the Cayman Islands (Uetz 2026). In Panama, *T. nigroluteus* Cope, 1861 and *T. mocquardi* Bocourt have been recorded (Köhler 2008; Ray and Ruback 2015), representing two distinct ecological and geographic lineages of the genus, with *T. nigroluteus* primarily associated with Caribbean drainages and *T. mocquardi* occurring mostly along the Pacific slope. *Tretanorhinus* typically occurs in lowland rainforests and coastal mangroves, where it prefers calm, shallow bodies of freshwater or brackish water with abundant aquatic vegetation. It is predominantly nocturnal, remaining submerged or concealed among vegetation during periods of activity (Cope 1861; Villa 1969; Savage 2002; González and González 2016; Melgar-Martínez et al. 2022; Solór-

zano 2022; Uetz 2026). However, little information is available regarding its ecology, distribution, and diet (Köhler 2008; Jaramillo et al. 2010; Lotzkat 2014; Ray 2017; Batista and Miranda 2020). Therefore, we present updated data on their distribution, including species distribution modeling, morphological differences, ecology, and behavior, based on both *in situ* and *ex situ* observations of *Hydromorphus* and *Tretanorhinus* in Panama.

Methods

Literature review

We conducted a comprehensive literature review to compile reports from Panama of the snakes of the genera *Hydromorphus* and *Tretanorhinus*, including habitat use and natural history data, and to develop a dichotomous key.

Searches were performed in Google Scholar in English, Spanish, and Portuguese to identify articles published up to June 2025, using the following keywords: *Hydromorphus*, *Hydromorphus concolor*, *Hydromorphus dunni*, *Hydromorphus Panama*, *Tretanorhinus*, *Tretanorhinus mocquardi*, *Tretanorhinus nigroluteus*, *Tretanorhinus variabilis*, *Tretanorhinus taeniatus*, and *Tretanorhinus Panama*. We also obtained distribution records from the Global Biodiversity Information Facility (GBIF 2025a, 2025b), including citizen-science observations from iNaturalist, restricting the dataset to records classified as "Research Grade," each of which was individually reviewed for quality control.

Collection specimens

We examined preserved specimens from the Círculo Herpetológico collection (CH) at the Smithsonian Tropical Research Institute, Panama City, and the herpetology museum of the Universidad Autónoma de Chiriquí (UNACHI) to determine, through folidosis, the characteristics that would allow us to differentiate the species at a morphological level. All specimens examined correspond to records from the country, some of which are also available in GBIF.

Fieldwork

Live individuals of *Hydromorphus* and *Tretanorhinus* (23 in total) were recorded across multiple regions of Panama between 2000 and 2025 using two types of fieldwork: rapid assessments conducted in the context of Environmental Impact Assessments (EIAs) and wildlife rescue and relocation programs, which typically involve short faunal inventories within specific project areas (22 individuals); and general herpetofaunal surveys following standard search protocols (one individual).

Ex situ work

To document the feeding behavior of *T. nigroluteus*, we maintained an adult male, rescued in the town of Portobelo (Colón Province), under controlled captive conditions (scientific permit ARB/ARG-047-2023; MiAmbiente: Ministry of Environment). We aimed to evaluate whether feeding occurred diurnally or nocturnally and to increase knowledge on diet. The enclosure contained water, rocks, and leaf litter to simulate a natural stream-edge microhabitat. The individual had continuous access to water and remained fully aquatic throughout the experiment. Rocks were provided as terrestrial shelters. Light cycles followed natural conditions, with no additional artificial illumination.

Two prey item types were offered, consisting of common and abundant species of fish and anurans found in freshwater habitats within the natural range of *T. nigroluteus*. We provided widely distributed freshwater fish from the genera *Astyanax* (Characidae) and juvenile *Brycon* (Bryconidae), common in rivers, streams, and highly disturbed areas in Panama (Fuentes et al. 2025). Tadpoles were of the non-threatened *Rhinella horribilis* (Bufonidae) and *Engystomops pustulosus* (Leptodactylidae), widespread in both temporary and permanent bodies of water in altered environments and secondary forests (Ibáñez et al. 1999). Prey items were introduced at specific times, and the enclosure was checked approximately every 10 hours to record whether feeding had occurred.

Ecological niche modeling

All analyses were conducted in R version 4.5.2 (R Core Team 2023). We obtained 19 bioclimatic variables from the CHELSA database (Karger et al. 2023) at a spatial resolution of 4.5 km^2. All layers were processed in raster format, projected to the WGS84 coordinate system, and clipped to the political boundaries of Panama using the R packages raster (Hijmans et al. 2025) and dismo (Hijmans et al. 2024). Additionally, we incorporated a forest-cover and land-use raster from the Panamanian Ministry of Environment (2021) to qualitatively assess landscape context; however, this layer was not included in the modeling process.

To reduce multicollinearity among bioclimatic predictors, we applied a correlation-based selection procedure ("cortest") to generate subsets of uncorrelated variables under varying correlation thresholds. Based on these subsets, we constructed seven candidate models (M1–M7), each containing four to seven non-collinear variables (M1: Bio1, Bio2, Bio3, Bio4, Bio7, Bio13, Bio14; M2: Bio1, Bio4, Bio7, Bio11; M3: Bio1, Bio2, Bio3, Bio5, Bio7; M4: Bio1, Bio5, Bio7, Bio13; M5: Bio1, Bio6, Bio9, Bio12; M6: Bio1, Bio2, Bio7, Bio12; and M7: Bio1, Bio2, Bio3, Bio14).

Species distribution models were developed using the MaxEnt package (Phillips 2021), combining species occurrence records with randomly generated 5000 background points (excluding known presences).

Models were run in "raw" output format to estimate the Relative Occurrence Rate (ROR), which was normalized to a 0–1 scale and interpreted as the relative probability of presence. Binary presence–absence maps were derived using the maximum sensitivity plus specificity (MaxSSS) threshold. Model performance was assessed via k-fold cross-validation, and predictive accuracy was evaluated using the Area Under the Curve (AUC) metric (Fielding and Bell 1997; Jiménez-Valverde 2012). AUC values ≥ 0.7 were considered indicative of good model performance (Manel et al. 2001).

Processing and identification of parasites

We kept in captivity one individual of *Tretanorhinus nigroluteus* that exhibited a parasitic infection detected through a subcutaneous cyst. The parasite was removed through a small incision in the skin following standard protocols, and the wound was treated with 10% iodine. The parasite found in the subcutaneous region was placed in 2 mL Eppendorf tubes containing 95% ethanol for later identification. The tail and head sections were then separated for morphological identification. Both sections were cleared following the protocol of Seinhorst (1962), using a mixture of 99.5% glycerin and 95% ethanol, and allowed to evaporate over 24 hours. Subsequently, internal and external structures were observed under a light microscope (Olympus CX43 with Olympus DP28 camera), using the dichotomous keys provided by Mazzone et al. (2019) and Rahmati-Holasoo et al. (2024) as references.

Taxonomic key

We used Köhler's taxonomic key (Köhler 2008) to guide identification up to the genus level. From that point, we constructed a dichotomous key based on morphological characters that we found and considered most relevant for distinguishing between the two genera.

Results

We provide an updated distribution for two aquatic snake taxa in Panama based on fieldwork conducted across diverse regions of the country, including Bocas del Toro, Coclé, Chiriquí, Colón, Darién, Panamá, Panamá Oeste, Veraguas, and the Ngäbe-Buglé Comarca, reflecting broad geographic coverage.

Based on our literature review, the only record of *Hydromorphus dunni* corresponded to the holotype from the original description. We increased the number of records by seven additional individuals (a 700% increase). For *H. concolor*, we added 16 new records (a 133% increase); for *Tretanorhinus mocquardi*, six (a 100% increase); and for *T. nigroluteus*, five (a 27.8% increase; Suppl. material 1).

Below, we present brief descriptions, including morphological differences among the species of each genus. These differences are further illustrated by a dichotomous key covering all species of both genera, including the two *Tretanorhinus* species that do not occur in Panama. The species accounts also include ecological and dietary information, as well as distribution maps based on both published and new records, documenting the first record of parasites in *T. nigroluteus*. Finally, a brief species distribution modeling section is provided for each taxon.

Hydromorphus concolor (Peters, 1859)

Morphology. We support the two morphological variations proposed by Savage and Donnelly (1988; Fig. 1A, B) and highlight the presence of an enlarged loreal scale in contact with both the eye and the upper preocular scale as an important character (Fig. 1C). We examined 13 specimens (11 live and two in collections). In Panama, only the variant illustrated in Figs 1B, 2A, B was observed.

Distribution. Type locality: Agua Clara, Chagres River, Colón Province.

The species is distributed at low to moderate elevations, from Guatemala to central Panama (Villa 1990; Savage and Donnelly 1988). In Panama, it has been recorded in Colón Province (Fuentes et al. 2023), Panamá Oeste Province (Ibáñez et al. 1996; Ray and Ruback 2015), Panamá Province (Barrio-Amorós et al. 2023), and Santa Fe National Park, Veraguas Province (Lotzkat 2014). We report the species for the first time from the Ngäbe-Buglé Comarca (Ciénaga Mono, 8.4867°N, 81.6850°W) and Coclé Province (Petaquilla, 8.7889°N, 80.6509°W; Fig. 3, Suppl. material 1).

Ecology and ethology. *Hydromorphus concolor* is a predominantly nocturnal and semiaquatic species; it inhabits small streams in lowland and premontane forests (Villa 1990; Savage and Donnelly 1988). Its overall appearance and habits are notably similar to those of *Tretanorhinus nigroluteus* (Peters 1859; Solórzano 2022). The diet is specialized, consisting of fish, frogs (Obst et al. 1988), and small freshwater crabs (Savage and Donnelly 1988), which may reflect an evolutionary adaptation (Savage and Donnelly 1988). The author MU has observed this species in Valle de Antón (Coclé Province, Panama) feeding on small shrimps of the genus *Atya*.

Its reproductive biology remains largely unknown. The species has been documented as oviparous, with clutches of up to eight eggs and an estimated incubation period of approximately 94 days. Egg size ranges from 33 to 44 mm in length and from 14 to 16 mm in width, with a mass of 6.1–6.6 g. Hatchling length ranges from 161 to 173 mm, with a mass of 3.9–4.5 g (Solórzano 2022).

Only one case of predation has been published, involving the false coral snake *Erythrolamprus bizona* Jan, 1863 in Costa Rica (Savage 2002). A similar observation was reported by MU (2015), who documented *Hydromorphus concolor* being regurgitated by *E. bizona* in El Valle de Antón, Coclé Province, Panama (8.5932, –80.1229).

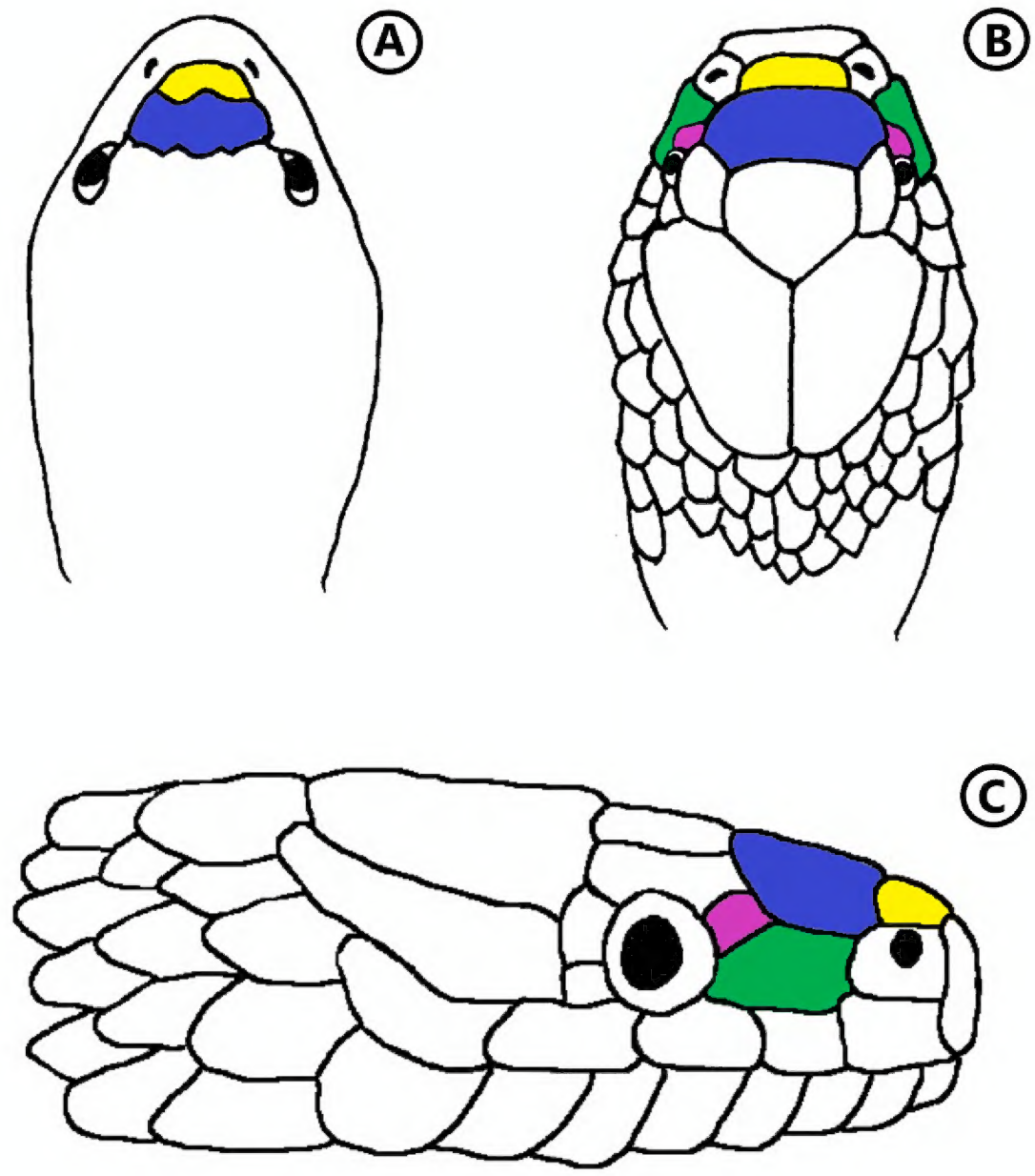

Figure 1. Head scale variations in *Hydromorphus concolor*: single internasal (yellow), single prefrontal (blue), extended loreal (green), and preocular (pink). **A.** Dorsal view of specimen KU 190961, Guatemala, modified from Savage and Donnelly (1988); **B.** Dorsal view of specimen CRE 3014, Costa Rica, modified from Savage and Donnelly (1988); **C.** Lateral view.

Figure 2. *Hydromorphus concolor* **A.** Portobelo National Park; **B.** Petaquilla, Coclé.

Hydromorphus dunni Slevin, 1942

Morphology. We provide a revision of the head morphology of *Hydromorphus dunni* as described by Savage and Donnelly (1988), who illustrated a fused internasal scale. In contrast, the original photograph by Slevin (1942) shows two internasals and three prefrontals. We examined seven specimens from seven different localities in Panama (see Suppl. material 1) to evaluate morphological variation, which led us to propose three pileus arrangements for this species: (1) two internasals + three prefrontals (Slevin 1942; Fig. 4A, holotype from Boquete, Chiriquí); (2) two internasals + one prefrontal (this study; Figs 4B, 5A, C, D, from Donoso, Colón; Santa Fe, Veraguas; Cerro Turega, Coclé); and (3) two internasals + two prefrontals (this study; Figs 4C, 5B, from Río Macho de Monte, Chiriquí Highlands). All arrangements are characterized by a loreal scale separated from the eye and an elongated preocular scale in contact with the supraocular and the third supralabial scales (Fig. 4D).

Distribution. Type locality: Boquete, Chiriquí Province, Panama.

Hydromorphus dunni was known exclusively from its type locality in the "southwestern Panamanian highlands in the premontane zone (approximately 1250 m)," as reported by Savage and Donnelly (1988), and only a single specimen (a holotype) had been recorded prior to this study. We report seven additional individuals: one from

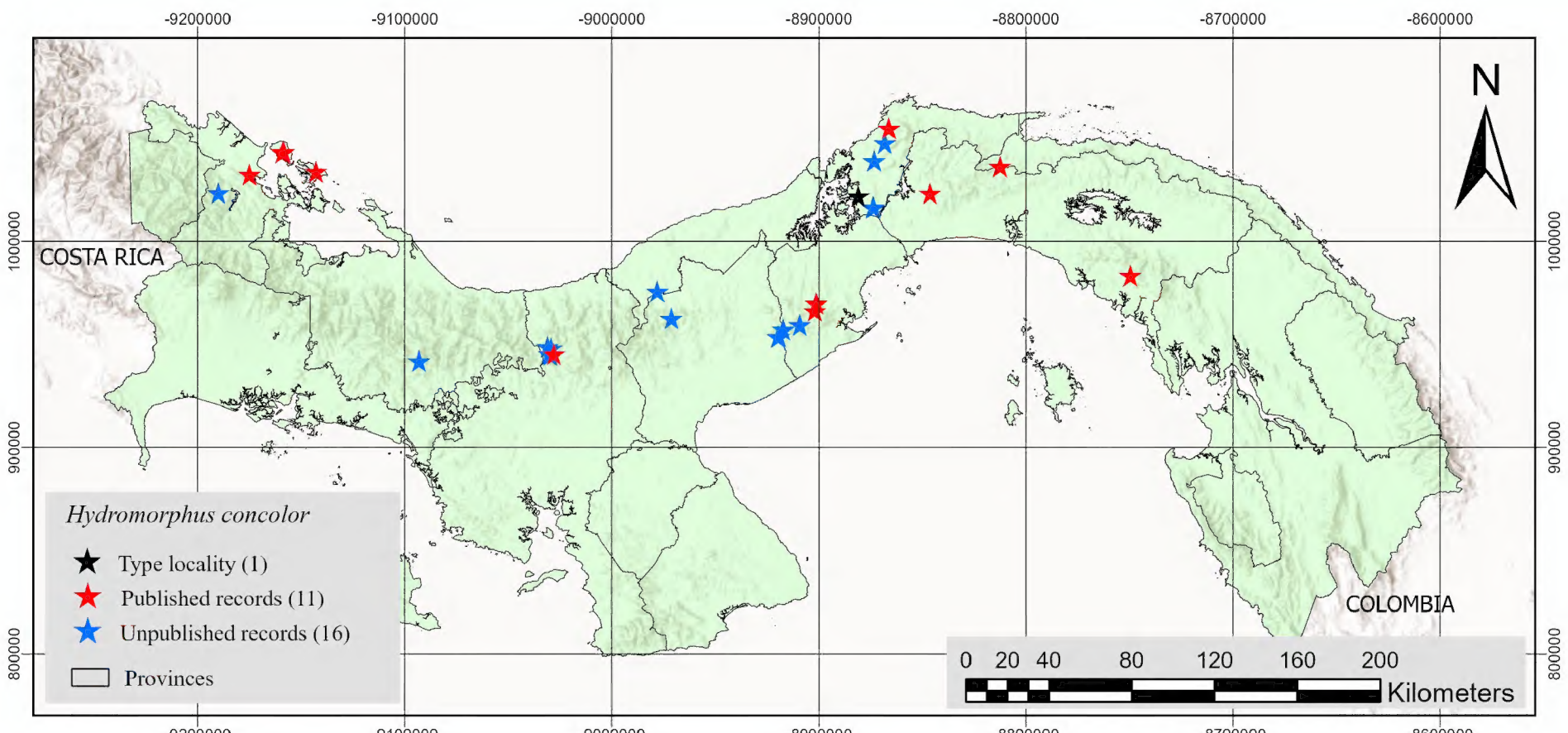

Figure 3. Distribution of *Hydromorphus concolor* in Panama.

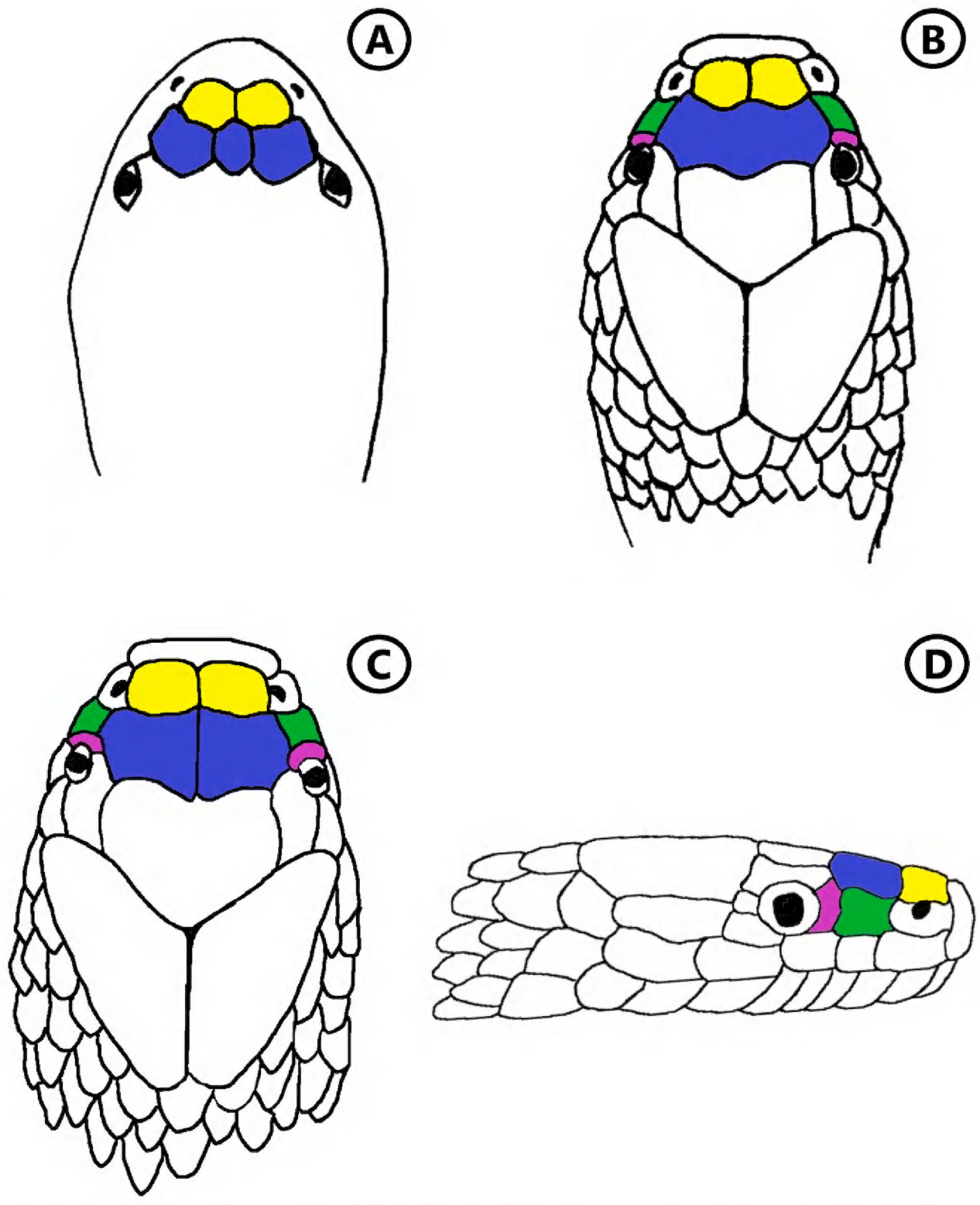

Figure 4. Variations in head scales of *Hydromorphus dunni*: internasals (yellow), prefrontals (blue), loreals separated from the eyes (green), and extended preoculars (pink). **A.** Dorsal view of specimen CAS 78939, Panama, modified from Savage and Donnelly (1988); **B.** Donoso, Colón; Santa Fe, Veraguas; Cerro Turega, Coclé; **C.** Río Macho de Monte, Chiriquí Highlands; **D.** Lateral view for all specimens in this study.

the Chiriquí Highlands (Río Macho de Monte); two from Santa Fe National Park, Veraguas (Quebrada Ñoli and Alto de Piedra); two from Coclé (Cerro Turega); and two representing the most distant range extensions. The sixth individual extends the known distribution by 228 km northeast to Donoso (Colón Province), while the seventh extends it by 273 km southeast to Altos de Campana National Park, which now represents the easternmost known locality for the species (Fig. 6, Suppl. material 2).

Ecology and ethology. Individuals of this species, like those of its congener *Hydromorphus concolor*, are medium-sized (up to 482 mm in total length) and exhibit aquatic habits, being primarily active at night in or near small freshwater streams in lowland and premontane forests (Savage and Donnelly 1988). Detailed information on the diet of *H. dunni* is not available. However, a possible dietary shift toward smaller, soft-bodied prey has been suggested for the genus *Hydromorphus*, based on morphological variation in the development of the mental groove, which may be related to this dietary adaptation (Savage and Donnelly 1988).

The species is oviparous, but clutch size and egg dimensions remain unknown (Köhler 2008). No cases of predation have been recorded. Nonetheless, birds associated with aquatic environments, freshwater turtles, and ophiophagous snakes such as *Micrurus* are likely potential predators.

Tretanorhinus mocquardi Bocourt, 1891

Morphology. Individuals of *Tretanorhinus mocquardi* are characterized by a color pattern composed primarily of longitudinal stripes along the dorsum and flanks. They possess 19 dorsal scale rows anteriorly, which reduce toward the posterior part of the body. The number of ventral scales ranges approximately from 166 to 177 and subcaudals from 69 to 85, with sexual dimorphism present. The head bears a single prefrontal scale (although rare cases with two have been documented), one loreal scale, and two preoculars. The cephalic color pattern and scalation are typical of the genus *Tretanorhinus*, reflecting

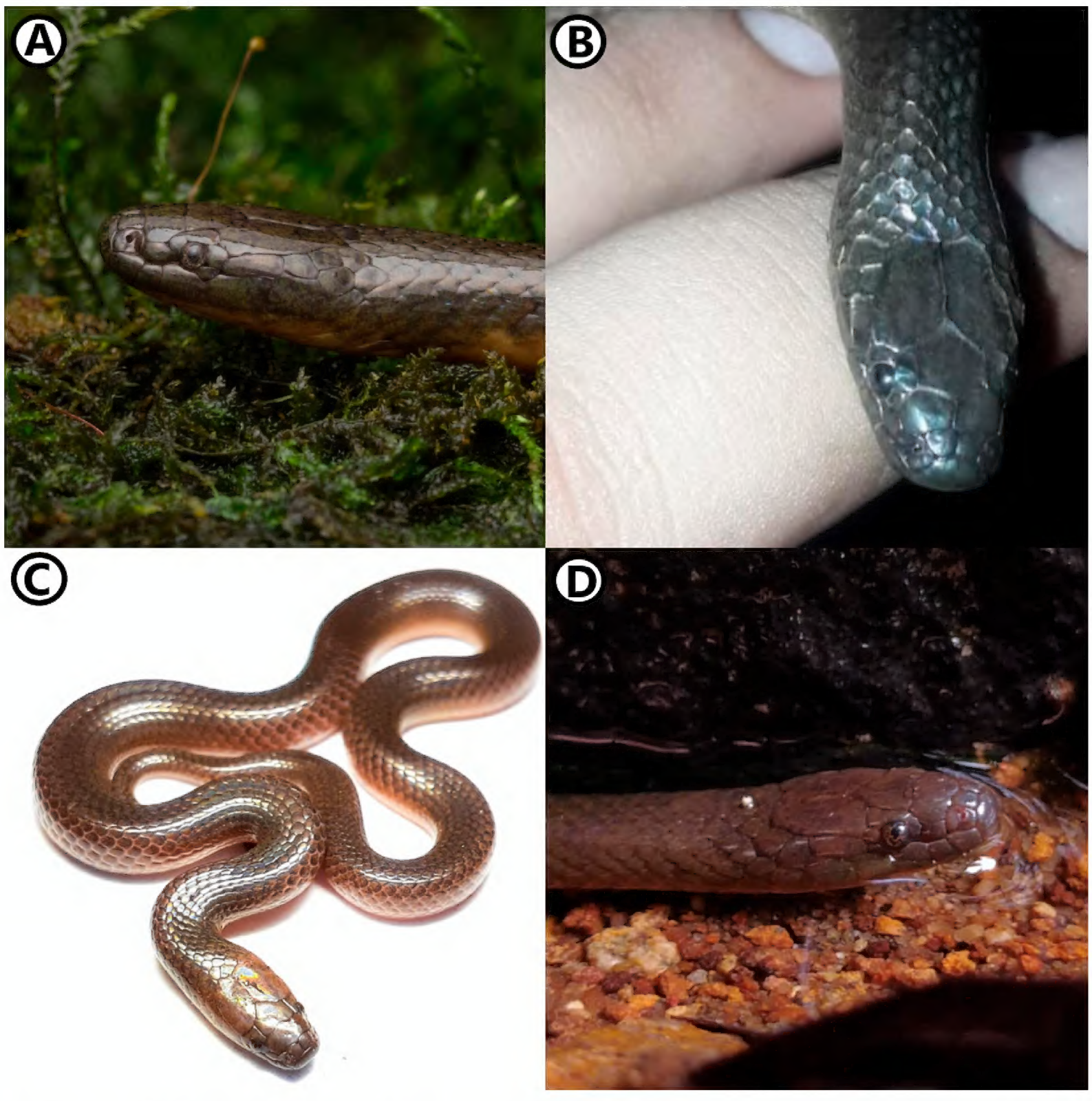

Figure 5. Variations of *Hydromorphus dunni* in Panama. **A.** Alto de Piedra, Santa Fe (two internasals + one prefrontal); **B.** Chiriquí Highlands (two internasals + two prefrontal); **C.** Cerro Turega, Coclé (two internasals + one prefrontal); **D.** Donoso, Colón, and Altos de Campana National Park (two internasals + one prefrontal).

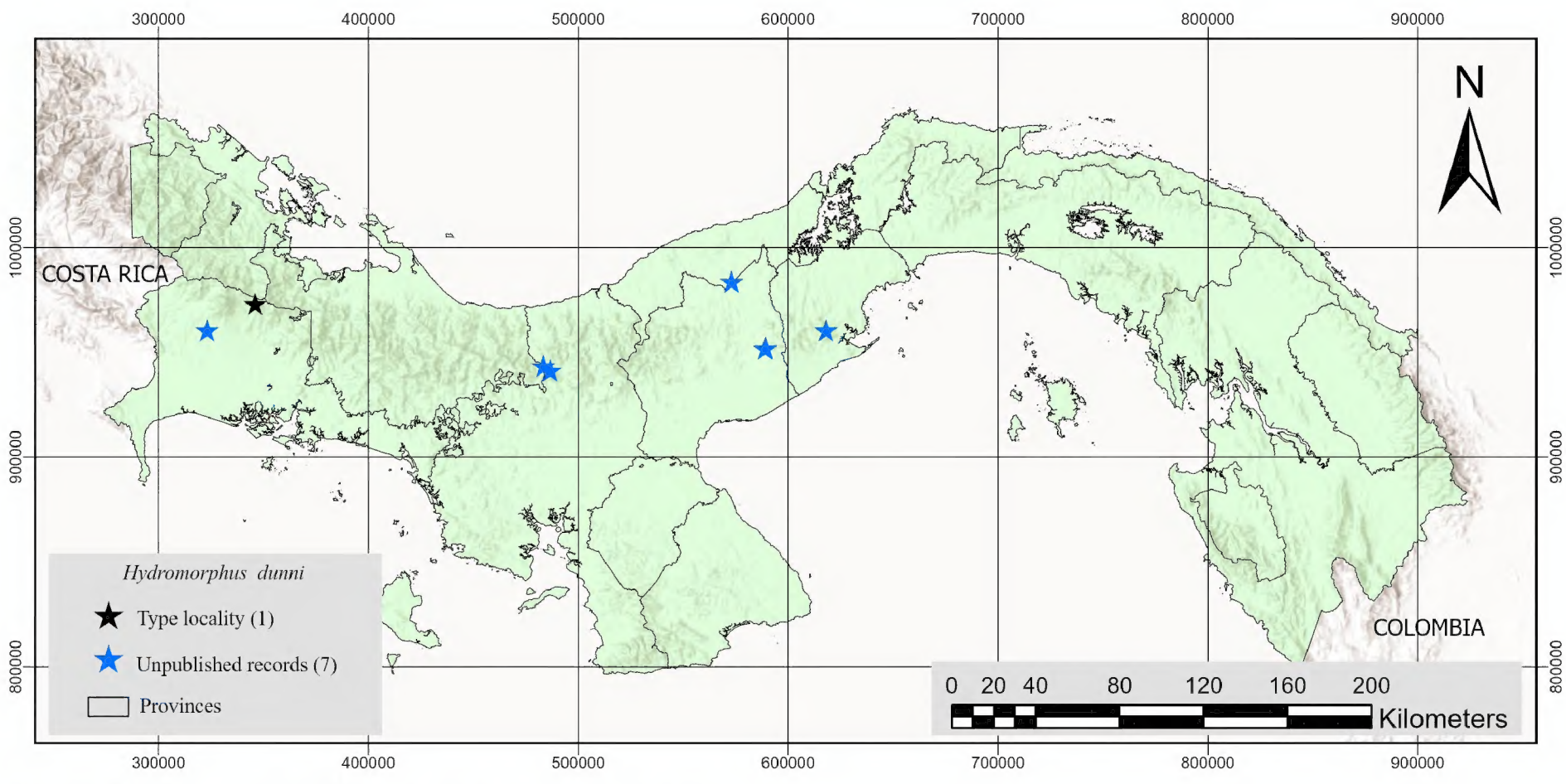

Figure 6. Distribution of *Hydromorphus dunni* in Panama

adaptations to an aquatic lifestyle. Coloration usually includes a dark vertebral stripe and a well-defined lateral stripe along the fourth dorsal scale row, with the lower rows noticeably lighter (Dunn 1939; Fig. 7A–D).

Distribution. Type locality: Panama City, corrected by Dunn (1939).

Individuals of *Tretanorhinus mocquardi* occur primarily along the foothills of the Pacific slope, with a distribution extending from the Panama Canal Zone southeastward to the Pacific coast of Colombia and Ecuador (Dunn 1939; Barquero and Arguedas 2019; Vásquez-Restrepo 2020). In Panama, the species has been recorded in Panamá Oeste (Ray and Ruback 2015), the Panama Canal Zone, and Panamá and Colón provinces (Dunn 1939). Here, we report *T. mocquardi* for the first time from Chepigana and Tucutí (Darién Province), Pedro González Island (Panamá Province), and Leones Island (Veraguas Province). The latter represents the southwesternmost known record, extending the species' known range 146 km southwest of the previous record (Fig. 8, Suppl. material 1).

Ecology and ethology. *Tretanorhinus mocquardi* is an aquatic snake associated with a variety of freshwater and brackish environments, including rivers, streams, lagoons, estuaries, and mangroves (Cisneros-Heredia 2005). The species prefers habitats with muddy or rocky substrates and abundant aquatic vegetation (Barquero and Arguedas 2019). It is mainly distributed along the Pacific slope, from the Panama Canal Zone to the Pacific coast of Colombia and Ecuador (Dunn 1939; Barquero and Arguedas 2019; Vásquez-Restrepo 2020). *Tretanorhinus mocquardi* occurs in sympatry with *T. taeniatus* in Esmeraldas Province, Ecuador, and *T. nigroluteus* in the Chocó Department, Colombia (Barquero and Arguedas 2019; García-Cobos and Vásquez-Restrepo 2022). Due to its nocturnal and elusive habits, the species is difficult to study, which is reflected in the limited information available on its biology (Savage 2002; Barquero and Arguedas 2019).

The species is oviparous, laying six to nine eggs (Campbell 1999; Köhler 2008). Its predators remain unknown; however, Villa (1969) suggested that water-associated birds, turtles, snakes, and invertebrates (such as crabs) may act as potential predators. Published information on the diet of *Tretanorhinus mocquardi* is virtually nonexistent (Barquero and Arguedas 2019), highlighting the need for further research to improve understanding of the species' trophic ecology. Nonetheless, its diet may resemble that of its congeners.

Tretanorhinus nigroluteus Cope, 1861

Morphology. *Tretanorhinus nigroluteus* is characterized by having 17–21 dorsal scale rows along the body, with two prefrontals in the cephalic scalation. The number of ventral scales ranges approximately from 133 to 148, while subcaudals vary from 63 to 80 in males and from 56 to 68 in females, indicating moderate sexual dimorphism. Dorsal coloration displays a distinctive pattern: in most adult individuals, a mid-dorsal line composed of alternating dark spots is present, with each spot occupying nearly the entire surface of a single scale (Dunn 1939; Fig. 9).

Distribution. Type locality: Aspinwall, Panama, corrected by Peters and Orejas-Miranda (1970).

This species has a wide distribution along the Atlantic coast, extending from southern Mexico to Colombia, and occurs on offshore islands such as the Bay Islands (Honduras) and Great Corn Island (Nicaragua; Dunn 1939; Villa 1969; Barquero and Arguedas 2019). In Panama, its distribution extends from the western region to Costa Arriba de Colón and the former Panama Canal Zone (Dunn 1939; Villa 1969, 1970; Ray and Ruback 2015; González

Figure 7. Two morphotypes of *Tretanorhinus mocquardi* from Chepigana, Darién. **A, B.** Morphotype 1; **C, D.** Morphotype 2.

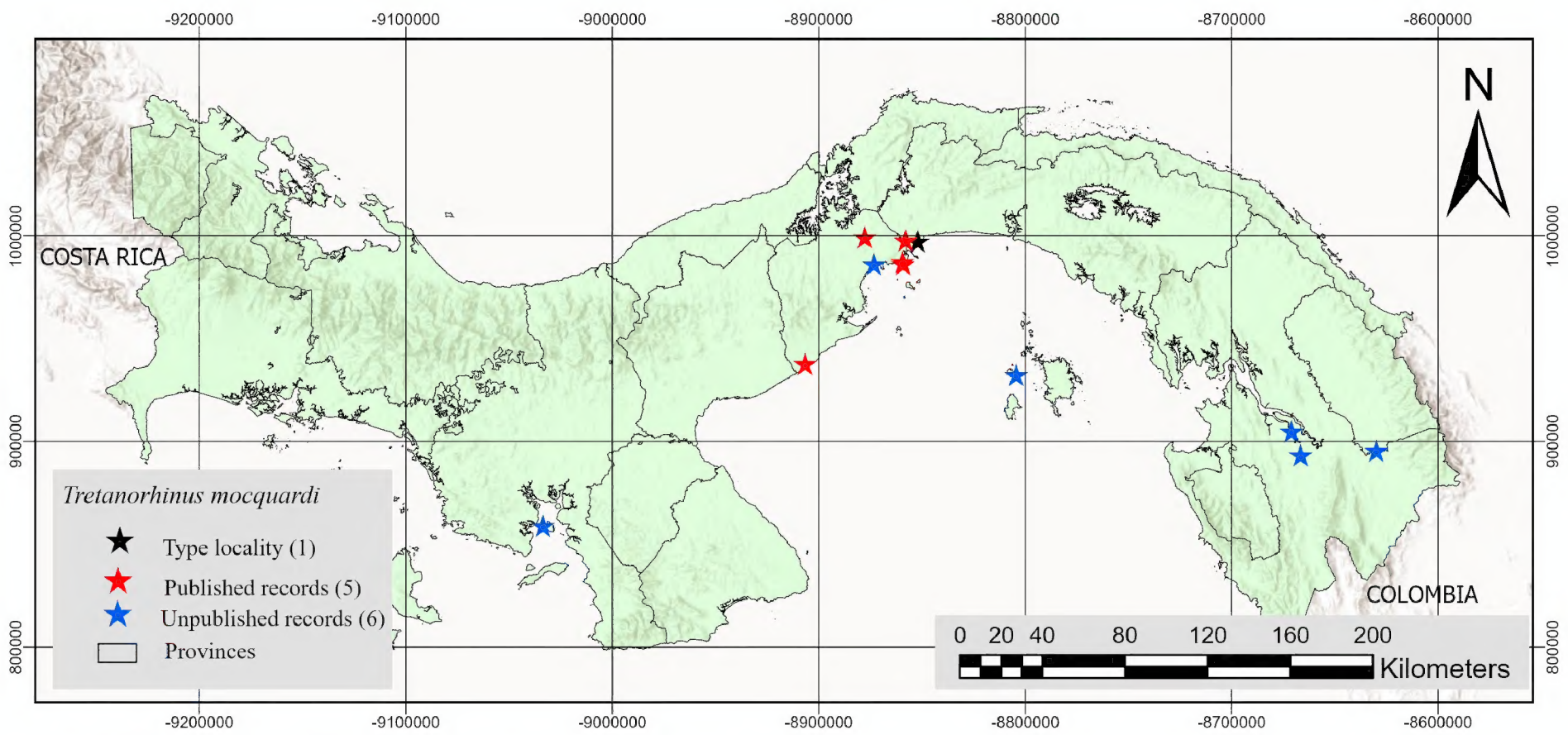

Figure 8. Distribution of *Tretanorhinus mocquardi* in Panama.

and González 2016). We report *Tretanorhinus nigroluteus* for the first time from the Teribe and Changuinola rivers (Bocas del Toro Province). Based on Dunn's (1939) morphological description, we identified the subspecies *T. nigroluteus lateralis* from Donoso (Colón Province) and *T. nigroluteus nigroluteus* from Portobelo National Park (Colón Province), thereby extending the known distribution of the species by 29 km northeast of its previously documented range.

We corrected the locality of specimen MCZ Herp: R-2717, originally listed in the Museum of Comparative Zoology (MCZ), Harvard University database as "Chiriquí Province" (georeference: 8.3772°N, 82.1988°W; error radius: 96949 m), assigned by José Rosado on 8 April 2021 using GEOLocate. The correct coordinates are 9.0718°N, 79.6594°W, corresponding to "Obispo Station, on railway," Panama (Fig. 10, Suppl. material 1).

Figure 9. *Tretanorhinus nigroluteus* morphotypes. **A–C.** Portobelo National Park; **D.** Donoso, Colón.

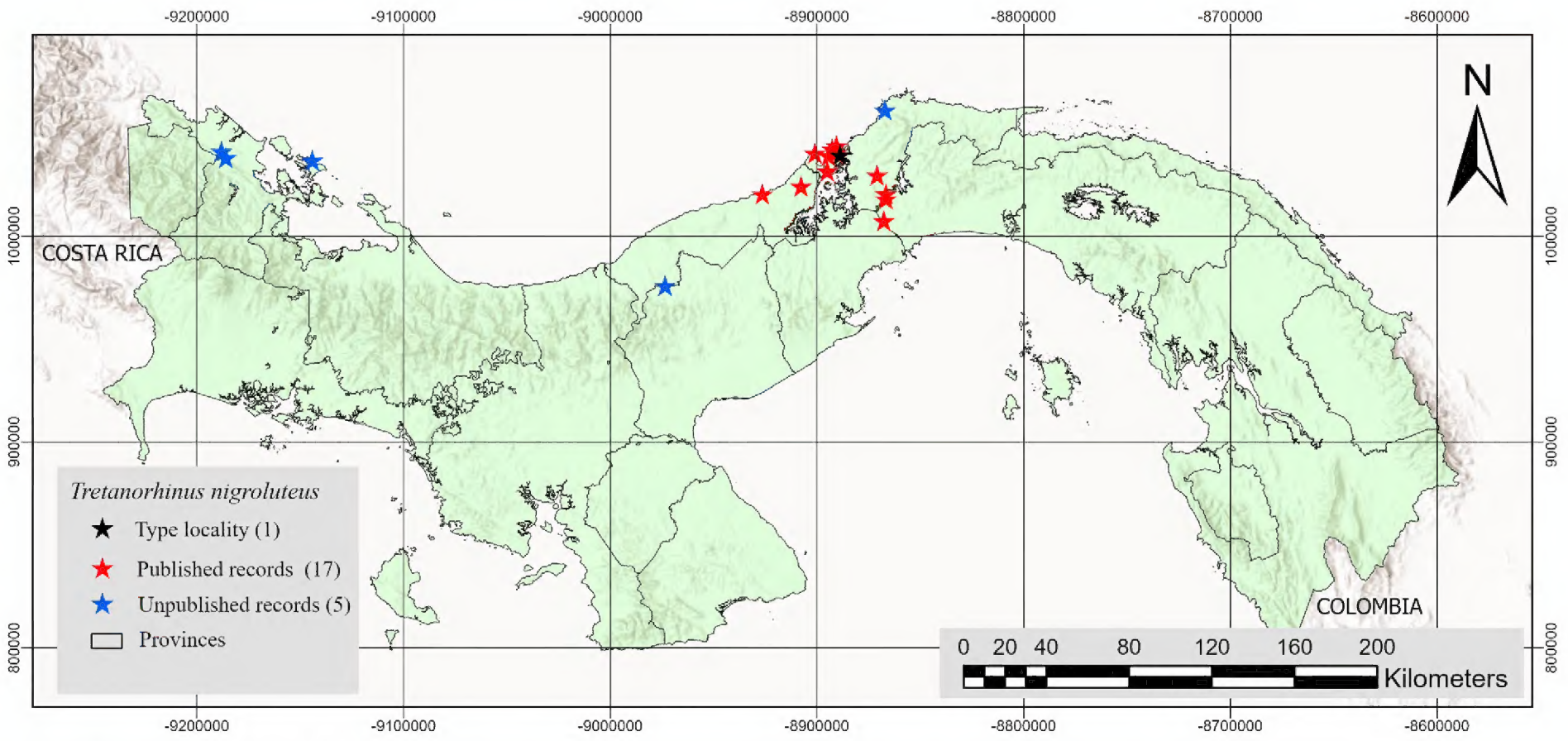

Figure 10. Distribution of *Tretanorhinus nigroluteus* in Panama.

Ecology and ethology. *Tretanorhinus nigroluteus* is a strictly aquatic species, generally found submerged in slow-moving rivers and streams with muddy substrates, particularly along shallow margins of lakes, lagoons, and brackish estuaries with aquatic vegetation or green algae, which appear to characterize its optimal microhabitat. The species is rarely observed on land or basking (Villa 1970). However, González and González (2016) reported an individual moving along a road through a mangrove area; we rescued a specimen in vegetation adjacent to a stream in the town of Portobelo, Colón Province. Water salinity and pH do not appear to be major limiting factors, and water temperatures at sites where individuals have been found range from 24.5 to 27.5 °C (mean 26.0 °C; Villa 1970), although further research is needed.

Tretanorhinus nigroluteus is crepuscular and nocturnal. During the day, individuals shelter in mud, roots, or vegetation, exposing only the snout for respiration (Villa 1970;

Barquero and Arguedas 2019). When disturbed, they dive and seek refuge in rock crevices (Dunn 1939; Villa 1970). The species occurs at low to moderate elevations, typically below 500 m above sea level, although it has been reported at 1200 m in Matagalpa, Nicaragua, where it inhabits isolated ponds or calm sections of rivers (Villa 1970).

The diet of *T. nigroluteus* consists primarily of aquatic animals such as fish, frogs, and tadpoles (Villa 1970; Heimes 2016; Solórzano 2022). Prey items documented *in situ* include *Poecilia sphenops* Valenciennes, 1846, *Gambusia nicaraguensis* Günther, 1866, gobiid fishes, and tadpoles of *Rhinella* and *Incilius* (Villa 1970). In captivity, Villa (1970) documented that the species accepts a wide variety of fish, including *Alfaro cultratus* (Regan, 1908), *Awaous transandeanus* (Günther, 1861), *Bathygobius soporator* (Valenciennes, 1837), *Amatitlania nigrofasciata* (Günther, 1867) which has also been recorded in the wild, *Eleotris pisonis* (Gmelin, 1789), *Poecilia reticulata* Peters, 1859, *Priapichthys annectens* (Regan, 1907), *Rhamdia* sp., and *Cynodonichthys isthmensis* (Garman, 1895), as well as adult amphibians such as *Craugastor fleischmanni* (Boettger, 1892), *Dendropsophus microcephalus* (Cope, 1886), *D. phlebodes* (Stejneger, 1906), *Scinax staufferi* (Cope, 1865), *Leptodactylus fragilis* (Brocchi, 1877), *L. melanonotus* (Hallowell, 1861), *Lithobates palmipes* (Spix, 1824), *L. vibicarius* (Cope, 1894), and *L. warschewitschii* (Schmidt, 1857). A recent record of Melgar-Martínez et al. (2022) further expanded the known diet of the species to include freshwater snails *Pachychilus largillierti* (Philippi, 1843).

While being held in captivity for experimental purposes (Fig. 11A), the individual *T. nigroluteus* remained submerged throughout the entire observation period, partially or fully exposing only the head (Fig. 11B). When fish (*Astyanax* sp. and juvenile *Brycon* sp.) were offered overnight (20:00–08:00 h on 19–20 June 2025), no feeding was observed. In contrast, tadpoles (*Rhinella* sp. and *Engystomops pustulosus*) offered on 25 June (five individuals) were consumed within approximately 15 hours, and an additional six tadpoles were consumed on 26 June. To determine whether feeding also occurred during daylight hours, tadpoles were offered in the morning (08:00 h on 27 June and 10:00 h on 28 June, respectively). In both cases, all tadpoles offered (eleven and fifteen individuals) were consumed before 18:00 h. The snake began shedding on 28 June and successfully completed the process on 3 July. When three tadpoles and one metamorph were offered on 3 July (19:20 h), no feeding was observed until 14 July, when all tadpoles were consumed. The metamorph remained uneaten until 15 July, when it was found dead. On 16 July, during enclosure cleaning, we observed the carcasses had been consumed, suggesting that *T. nigroluteus* may exhibit necrophagy under certain conditions.

Tretanorhinus nigroluteus is oviparous with documented clutches of six to nine eggs (Köhler 2008; Solórzano 2022). Villa (1970) suggested that potential predators of this species include animals associated with aquatic ecosystems, such as herons and *Cochlearius* or *Tigrisoma* species, as well as turtles of the genera *Chelydra*, *Kinosternon*, and *Pseudemys*. However, there is currently no direct evidence supporting this hypothesis.

First report of a parasite in *Tretanorhinus nigroluteus*

Due to the clearing technique for the parasite specimen, the cephalic end of the worm revealed the esophagus and visible cephalic papillae (Fig. 12C), structures characteristic of parasites belonging to the genus *Eustrongylides* (Nematoda). Additionally, structures corresponding to a female (Fig. 12D) genital primordia were observed. Thus, the observed parasite corresponds to a third-stage larva. This constitutes the first Panamanian record of the nematode *Eustrongylides* (Ascaridida: Dioctophymidae) parasitizing a snake host and the first worldwide report of this parasite for *Tretanorhinus nigroluteus*.

Figure 11. Diet study of *Tretanorhinus nigroluteus*. **A.** Microhabitat prepared for the individual; **B.** Typical position of the individual when not submerged among the leaf litter.

Key to aquatic snakes' species of the genera *Hydromorphus* and *Tretanorhinus*

The path leading to the *Hydromorphus* and *Tretanorhinus* genera according to Köhler (2008) follows these traits:

1b	Dorsal surface of head covered with large symmetrical shields	2
2b	Rostral shield normal (not protruding or pointed)	4
4b	Dorsal scales in an uneven number of rows at midbody	6
6b	Longitudinal mental groove present	7
7b	Combination of characters different from the following (leading to *Immantodes*): body extremely slender; head large and distinct from thin neck with large protruding eyes; 195–262 ventrals; 106–178 subcaudals	8
8b	Number of dorsal rows one head-length anterior to cloaca at least two rows fewer than at midbody	37
37b	Body without complete black rings, at most with dark bands that are not closed on the ventral side	39
39b	Scales of the vertebral row smooth or with only one keel	40
40a	Prefrontals fused into a single shield, or three prefrontal shields present	*Hydromorphus*
40b	Two prefrontal shields present	41
41b	One or more loreals, prefrontals not in contact with supralabials	45
45b	One or two loreals; no obvious lyre-shaped marking dorsally behind the head; number of dorsal rows at midbody variable	46
46b	Cloacal scute divided	56
56b	23 or fewer dorsal rows at midbody	61
61b	Dorsal scales keeled	62
62a	Nostrils directed dorsolaterally	*Tretanorhinus*

Key for *Hydromorphus* and *Tretanorhinus* taxa

1	Dorsal scales smooth	*Hydromorphus* (2)
–	Dorsal scales keeled	*Tretanorhinus* (3)
2	One internasal and one prefrontal shield; one loreal shield in contact with the eye; one preocular shield situated above the loreal	*H. concolor*
–	Two internasals; one to three prefrontals; one loreal not in contact with the eye; one elongated preocular in contact with the supraocular and the third supralabial	*H. dunni*
3	Dorsum with longitudinal lines	4
–	Dorsum without longitudinal lines	5
4	Posterior chin shields in contact; one or two prefrontals	*T. mocquardi*
–	Posterior chin shields separated; three prefrontals	*T. taeniatus**
5	Posterior chin shields separated	*T. variabilis**
–	Posterior chin shields in contact	*T. nigroluteus* (6)
6	Two loreals; two preoculars	*T. n. nigroluteus*
–	One loreal, three preoculars	*T. n. lateralis*

Ecological niche modeling

Forest habitats in Panama are dominated by mature and secondary broadleaf forests, particularly along the Pacific slope, interspersed with areas of herbaceous vegetation, shrublands, and human-populated zones (Fig. 13A). Within this landscape context, ROR predictions for *H. dunni* (Fig. 13B1) are concentrated primarily in humid sectors with continuous forest cover in western Panama and the central Caribbean, with low suitability in open or heavily disturbed landscapes. For *T. nigroluteus* (Fig. 13B2), areas of highest probability are located mainly along the Caribbean slope, where secondary and mature forests predominate, although suitability is disrupted in agricultural and human-populated areas. *Tretanorhinus mocquardi* (Fig. 13B3) exhibits a broader distribution pattern along the central axis of the country, associated with forest matrices that still retain connectivity, while suitability declines in fragmented savanna and cropland habitats. Finally, *H. concolor* (Fig. 13B4) shows high suitability in portions of the central cordillera and eastern Panama where humid forest patches persist, suggesting a stronger dependence on continuous forest cover and a lower tolerance for open or heavily transformed areas.

* Not occurring in Panama (*T. taeniatus* from Ecuador and *T. variabilis* from the Cayman Islands and Cuba) are included as a complement to the development of this key.

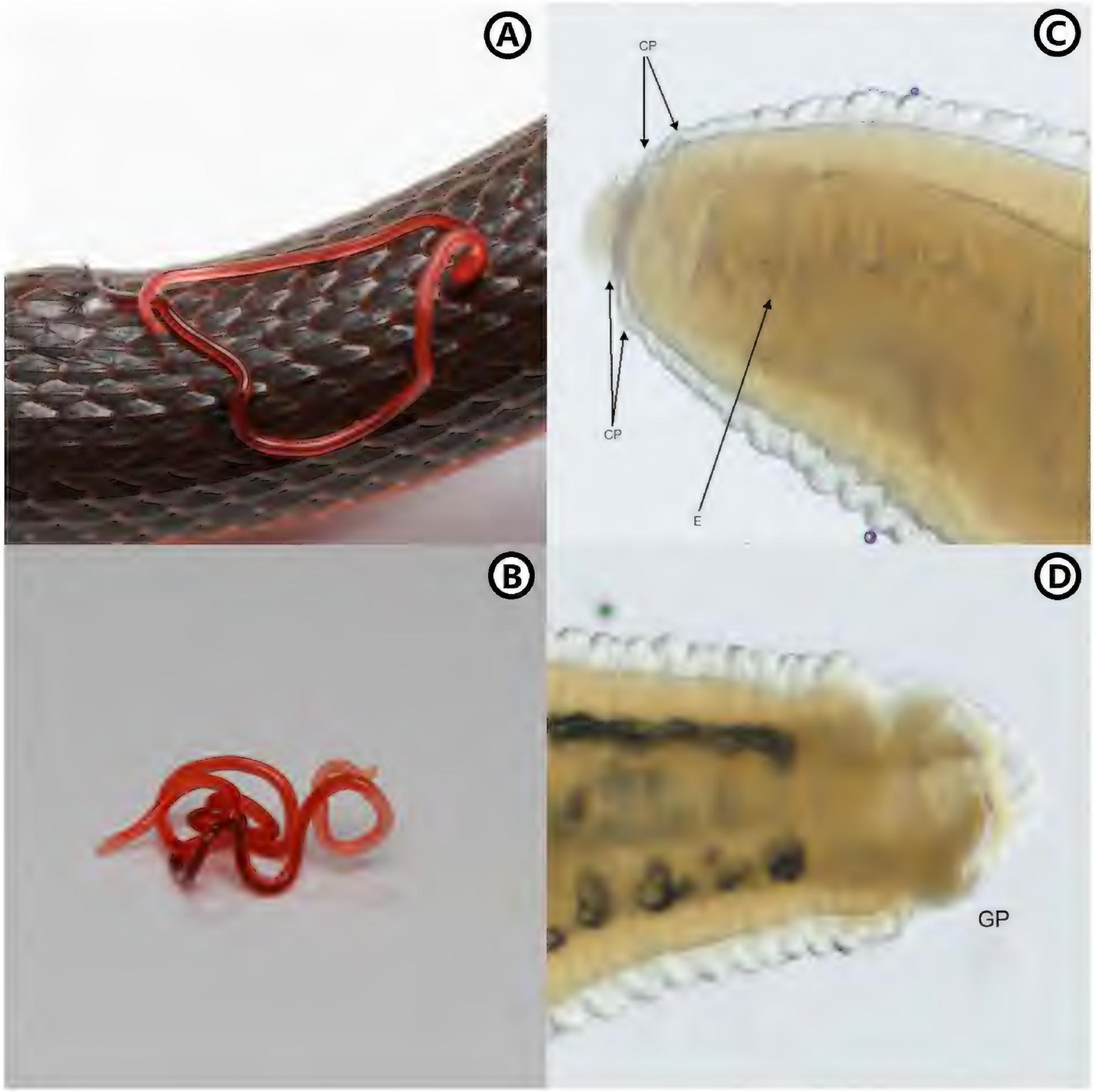

Figure 12. A. Parasite encysted in the subcutaneous region of the specimen of *Tretanorhinus nigroluteus*; **B.** Parasite extracted from the snake; **C.** Cephalic end of a *Eustrongylides* sp. larva showing the esophagus (E) and cephalic papillae (CP); **D.** Posterior end of a *Eustrongylides* sp. larva showing the female genital primordium (GP).

Taken together, the models showed good to excellent performance and revealed consistent patterns among species. In *H. dunni*, AUC_{all} model values ranged from 0.91 to 0.99, with Model 6 providing the best fit (M6, AUC = 0.99, MaxSSS ≈ 0.90). In this case, the resulting binary maps are highly restrictive, as only cells with the highest suitability values are classified as suitable habitat. This pattern indicates a narrow response to specific combinations of temperature and precipitation and a concentration of the potential distribution in the most favorable climatic environments.

For *T. nigroluteus*, $AUC_{all\ model}$ values ranged from 0.83 to 0.93, with Model 6 again emerging as the best model (M6, AUC = 0.93, MaxSSS ≈ 0.04). The very low threshold reflects that a large fraction of the continuous suitability gradient must be considered as present to maximize the sum of sensitivity and specificity, consistent with a broader or relatively continuous potential distribution across the landscape.

For *T. mocquardi*, $AUC_{all\ model}$ values ranged from 0.86 to 0.88, with Model 5 providing the best fit (M5, AUC = 0.88, MaxSSS ≈ 0.36). This result indicates an intermediate compromise in which the presence–absence conversion mainly retains areas of moderate to high suitability, suggesting a potential distribution less restricted than in *H. dunni* but more limited than in *T. nigroluteus*.

Finally, in *H. concolor*, $AUC_{all\ model}$ values ranged from 0.83 to 0.91, with Model 1 identified as the best model

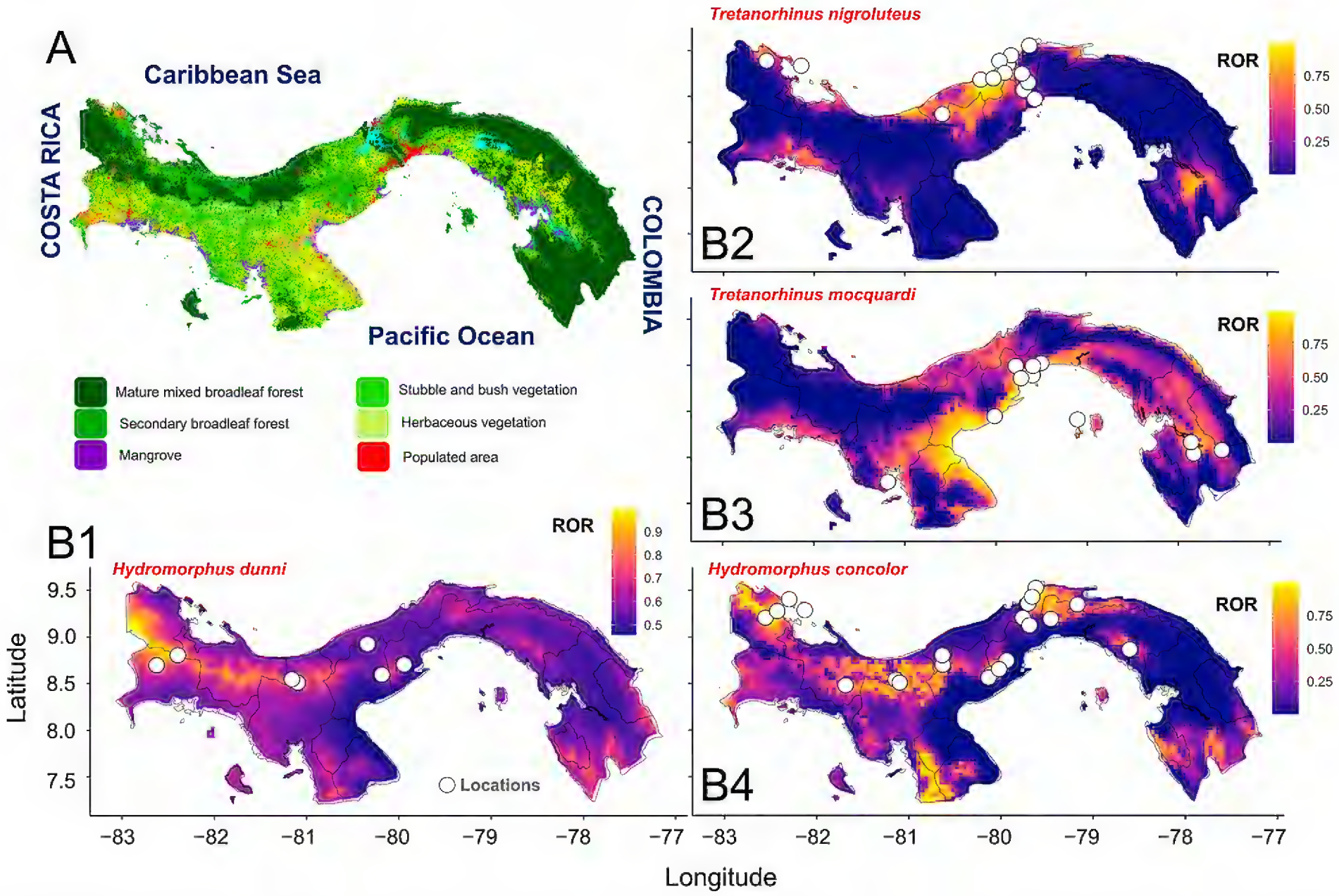

Figure 13. Land cover and Maxent-based potential distributions of four aquatic snakes in Panama. **A.** Forest cover map of the Republic of Panama; **B1–B4.** Relative Occurrence Rate (ROR) predicted for *Hydromorphus dunni* (**B1**), *Tretanorhinus nigroluteus* (**B2**), *Tretanorhinus mocquardi* (**B3**), and *Hydromorphus concolor* (**B4**). Warmer colors indicate higher ROR, and cooler colors indicate lower ROR. White circles represent occurrence records used to generate the models.

(M1, AUC = 0.91, MaxSSS ≈ 0.43). This intermediate threshold maintains a reasonable balance between omission and commission errors. Because M1 combines several temperature and precipitation variables (Bio1, Bio2, Bio3, Bio4, Bio7, Bio13, Bio14), its strong performance suggests that habitat suitability in *H. concolor* depends on the interaction between annual thermal variability and water availability. Overall, the selection of M1, M5, and M6 as optimal models for different species, together with their associated MaxSSS values, supports the idea that different components of climate, particularly thermal gradients and precipitation regimes, differentially modulate the potential distribution of these snakes and the degree of spatial restriction of habitats classified as suitable under the maximum sensitivity plus specificity criterion (Suppl. material 2).

Discussion and conclusion

This study provides important insights into the biology, distribution, and ecology of aquatic snakes of the genera *Hydromorphus* and *Tretanorhinus* in Panama, groups that have been historically underrepresented in the regional herpetological literature. Our findings substantially expand the known distribution ranges of the four species, documenting *Hydromorphus dunni* outside its type locality for the first time since its original description 84 years ago, as it was previously known only from its holotype (Slevin 1942; Savage and Donnelly 1988). Additionally, we provide new records for *T. mocquardi* and *T. nigroluteus*, extending their distributions into Darién, Veraguas, and Bocas del Toro (Fig. 7). These results highlight overlooked biogeographic connections and emphasize the need for continued surveys in underexplored regions.

We documented significant variation in the cephalic scalation of *H. dunni*, which allowed for the updating and refinement of previously accepted dichotomous keys through new combinations of morphological characters. For *H. concolor*, we concur with the two variations proposed by Savage and Donnelly (1988), which are consistent throughout its known distribution. In the case of *Tretanorhinus*, we agree with the diagnostic characters established by Dunn (1939) and propose no modifications.

Novel behavioral observations expand current knowledge of feeding ecology, particularly in *T. nigroluteus*. Our captive observations revealed necrophagy (scavenging), confirmed a preference for *Rhinella* tadpoles, and documented predation on *Engystomops pustulosus*. Evidence of diurnal activity further suggests ecological flexibility (Villa 1970). Collectively, these findings indicate that *T. nigroluteus* has an opportunistic diet, exploiting diverse prey across freshwater and brackish habitats, acting both as an ambush predator and an active hunter (Villa 1970).

Beyond feeding ecology, *T. nigroluteus* also participates in aquatic food webs as a host for nematodes of the genus *Eustrongylides*. This genus has previously been reported in three freshwater fish species in Panama: peacock bass, *Cichla ocellaris* Bloch & Schneider, 1801, *Vieja maculicauda* (Regan, 1905), both from Lake Gatun, and *Astyanax panamensis* (Günther, 1864) in Darién Province (Vasquez and Rogers 1992; Roche et al. 2010; González et al. 2026). *Eustrongylides* has a complex life cycle involving a wide range of intermediate and paratenic hosts, including oligochaetes and fishes and, less frequently, amphibians, reptiles, and mammals, with piscivorous birds acting as definitive hosts (Honcharov et al. 2022). Although infection by *Eustrongylides* in snakes is less common, it has been documented in aquatic species such as *Nerodia sipedon* (Linnaeus, 1758) in the United States (Bursey 1986), *Natrix natrix* (Linnaeus, 1758) and *Natrix tessellata* (Laurenti, 1768) in Europe (Yildirimhan et al. 2007; Sloboda et al. 2010; Yermolenko et al. 2022), *Helicops infrataeniatus* Jan, 1867 in Argentina (Veiga Pereira et al. 2021), and *Bothrops atrox* (Linnaeus, 1758) in Brazil (Conga et al. 2024). Our record underscores the role of snakes in aquatic trophic networks, particularly as hosts of parasitic organisms, and highlights the need for more systematic assessments of parasite diversity in these systems.

To contextualize these ecological observations at a broader spatial scale, we applied ecological niche models to infer habitat suitability and environmental limitation. These models integrate climatic, topographic, and distributional data to generate spatially explicit inferences (Elith and Leathwick 2009). When combined with forest cover maps and species-specific natural history information, such approaches help identify patterns of habitat availability and environmental constraints (Guisan and Thuiller 2005). Comparable studies on aquatic snakes using environmental niche modeling include Kornilev et al. (2023). Although exploratory in nature, our approach provides a robust approximation of potential habitat suitability for these species. *Hydromorphus dunni* shows a distribution linked to the central mountain range of western Panama, overlapping with *H. concolor* in central regions such as Santa Fe National Park, the Donoso region, and Altos de Campana National Park, where the two species may occur sympatrically. *Tretanorhinus nigroluteus* is broadly distributed along the Caribbean slope of Panama and reaches the Pacific via the Panama Canal, representing the only area where it may occur sympatrically with *T. mocquardi*. The latter species is distributed along the Pacific slope and may also occupy suitable habitats along the Darién coast. However, the limited number of occurrence records restricts the spatial precision of model predictions, and future efforts should prioritize additional field surveys to improve model calibration and validation.

These distributions largely reflect species-specific ecological preferences, with *H. concolor* primarily associated with freshwater environments (Savage and Donnelly 1988) and *Tretanorhinus* linked to brackish or marine-associated habitats (Villa 1970; González and González 2016). However, the Panama Canal constitutes an ecosystem artificially created more than a century ago that has facilitated faunal exchange between the Caribbean and Pacific slopes by significantly reducing natural ecological barriers and generating favorable environmental conditions for species dispersal. In the absence of this artificial corridor, the occurrence of *T. nigroluteus* in the Pacific or *T. mocquardi* in the Caribbean would be, in biogeographic terms, highly improbable. For *H. dunni*, its distribution is closely associated with freshwater bodies in ecosystems characterized by lower temperatures linked to the central mountain range of Panama, suggesting that its distribution is strongly constrained by environmental barriers, particularly those associated with altitudinal, climatic, and forest-cover gradients.

Due to their rarity, assessing the conservation status of these species is complex. Under Panamanian national legislation, *H. concolor* is categorized as Endangered (EN), whereas at the global level it is listed as Least Concern (LC) by the IUCN (2025). *Hydromorphus dunni* is classified nationally as Critically Endangered (CR) and as Data Deficient (DD) by the IUCN (2025). Owing to the scarcity of records prior to this study, the Panamanian Ministry of Environment did not assess species of the genus *Tretanorhinus* in 2016. Currently, *T. nigroluteus* is categorized as Least Concern (LC) and *T. mocquardi* as Data Deficient (DD) by the IUCN (2025). Based on the new data presented in this study, we propose listing both *H. concolor* and *H. dunni* as Vulnerable (VU) at the national level. At the global level, we recommend maintaining all species as Least Concern (LC), with the exception of *H. dunni*, which we suggest should be reassessed and potentially reclassified as Vulnerable (VU), given its ecological constraints and the increasing loss and degradation of habitat associated with mining, hydroelectric, and residential development projects within its distributional range.

Our findings highlight the ecological importance of these poorly known snakes, not only as predators and regulators of certain species' populations, but also as hosts within complex aquatic food webs. Moreover, they underscore new challenges for future research, particularly the incorporation of molecular studies to reconstruct the phylogeny of these groups and estimate divergence times among species. When integrated with the periods of formation of the Isthmus of Panama, these data will contribute to a better understanding of current distribution patterns and potential future scenarios for these species.

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Supplementary material 1

Distribution data

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Supplementary material 2

Additional figures

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